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The genus *Katelysia* (Bivalvia: Veneridae) in southern Australia

D. Roberts
Department of Zoology, The Queen's University, Belfast BT7 1NN, N. Ireland

ABSTRACT

General protein patterns revealed by isoelectric focussing support the view that *K. scalarina, K. rhytiphora* and *K. peroni* are distinct and valid species. Differences were revealed when the middle mantle folds of the three species were compared using SEM. Comparison of monthly gonad indices for the three species indicated distinct spawning periods with some overlap. *K. rhytiphora* spat were found bysally attached to live and empty adult shells in Oyster Harbour during March and April 1979. Zonation patterns of the three species showed considerable overlap, with *K. rhytiphora* and *K. peroni* occupying almost identical zones and *K. scalarina* extending higher up the shore.

INTRODUCTION

The genus *Katelysia* includes some of the most numerically abundant and productive shallow water suspension feeding bivalves along the south coast of Australia where it is frequently the major or dominant faunal component of shallow estuarine and marine embayments (Wells & Roberts, 1980; Wells & Threlfall, 1980; Coleman, 1982). Large fossil deposits of shells suggest that it has held this position for some time. At present members of the genus are distributed from Augusta, Western Australia in the west to Port Jackson, New South Wales in the east although formerly their distribution extended further northwards on the west coast as evidenced by extensive Pleistocene marine deposits on Rottnest Island (Nielsen, 1963). Their present distribution is believed to have resulted from geological changes over the last 4 to 5 thousand years.

Known colloquially as cockles, they are however venerids not cardiids, *Katelysia* densities may locally be very reduced due to human exploitation for food or fish bait. Although clearly illustrated and described by Cotton (1961) the three southern Australian species *K. scalarina* (Lamarck, 1818), *K. peroni* (Lamarck, 1818) and *K. rhytiphora* (Lamy, 1935) as *K. corrugata* (Lamarck, 1818) are not easily separated in samples from certain localities. Despite these systematic problems and its ecological and geological importance the genus has received scant attention over recent years. Nielsen (1963) was forced to omit *K. peroni* from her studies of *Katelysia* systematics because of limited material although she did provide useful information on synonyms, distributions and shell characteristics of this species.

The present report is a biological appraisal of *Katelysia* species based on a study, over one year, of populations in King George Sound, Western Australia and of occasional samples from other localities.

MATERIALS AND METHODS

Investigations were of four types:

1) Electrophoresis

Samples of whole *Katelysia* taken from Seine Bay, Augusta (34° 19'S, 115° 9'E), Oyster Harbour and Princess Royal Harbour, Albany (34° 57'S, 117° 54'E) Western Australia, and Great Bay, Bruny Island (43° 21'S, 147° 18'E) Tasmania were frozen and brought to Belfast via Sydney on dry ice in an insulated container. All samples were collected in July and August 1979. Individual entire soft tissues were homogenized with a few drops of Tris-HCl buffer to extract proteins. After high-speed centrifugation sample supernatants were subjected to polyacrylamide gel (PAG) iso-electric focussing for 1 h on a pH gradient of 3.5-9.5 at 25 watts. Gels were then fixed and stained for general proteins using Coomassie blue. Banding patterns were compared and bands counted. These were used to calculate coefficients of similarity (Sm) for the three species where

$$Sm = \frac{\text{number of bands of common mobility}}{\text{maximum number of bands in an individual}} \quad \text{(Ferguson, 1980)}$$

2) Anatomy

Internal features of several preserved specimens were compared after removal of the left valve. Certain differences between the posterio-ventral mantle margin soon became apparent during these dissections and portions of this region of the mantle were fixed in 4% glutaraldehyde (2 parts) and 1% O_sO_4 (1 part) for scanning electron microscopy (SEM) and processed routinely by alcoholic dehydration and critical point drying. Specimens were then mounted on aluminium stubs, coated with gold and examined on an I.S.I. Super Mini Scanning Electron Microscope (SEM) operating at 15 Kv.

3) Seasonal Population and Reproductive Changes

At approximately monthly intervals from September 1978 to August 1979 samples of *Katelysia* were taken from sites close to the pier at Albany in Princess Royal Harbour and Emu Point in Oyster Harbour. Samples were collected at low tide by sieving through a 2 mm mesh sieve, the top 8-10 cm of sediment from approximately the same region of the shore just below low water level where maximal overlap of species generally occurred (Wells & Roberts, 1980: Wells & Threlfall, 1980). Samples were fixed in 10% formalin. Subsequently shell length was measured to the nearest 0.1 mm using sliding vernier calipers and the gonad was removed for histological examination. Population size frequency distributions were constructed from the shell-length data. Reproductive tissues were dehydrated and embedded in paraffin wax, sectioned at approximately 8μ and stained in haematoxylin and eosin and examined microscopically. This enabled the gonad of each individual to be assigned an arbitrary numerical value from 0 for undifferentiated or spent gonads, to 4 for fully ripe gonads (Fig. 1). The average of these values for each sample gives a gonad index which is a useful guide to the reproductive state of bivalve population at any time (Seed & Brown, 1975). The sampling procedure resulted in unequal sample sizes for the different species. These ranged from as low as 5 for some samples of *K. rhytiphora* to as high as 200 plus for some samples of *K. scalarina,* a reflection of the relative proportions of the different species at the sampling points. Entire samples were used for size frequency distributions but smaller, more comparable sample sizes (between 5 and 20) were used for estimation of gonad indices.

4) Distribution

The vertical zonation of different *Katelysia* species at single sites in Princess Royal Harbour and Oyster Harbour are reported elsewhere (Wells & Roberts, 1980; Wells & Threlfall, 1980) and information from these sources pertinent to the present study is summarized below. Since the different *Katelysia* species showed considerable vertical overlap in distribution random samples were taken at selected sites in Oyster Harbour and Princess Royal Harbour for information on horizontal distribution of the three species.

RESULTS

1) Electrophoresis

Fig. 2 illustrates the results of isoelectric focussing experiments using PAGs on homogenized entire specimens of *Katelysia*. Some banding features were fairly consistent for each species, notably the pair of bands a_1a_2 for *K. scalarina* and the three bands $x_1x_2x_3$ for *K. peroni*. As the samples had been frozen for some time (up to 2 years) before electrophoresis and may have shown some deterioration in storage the maximum s_m values for each compared pair were taken as the most reliable values for the data obtained (Table 1). Nevertheless, useful comparisons may be drawn from the data presented in dendrogram form (Fig. 3). Interspecific comparisons suggest that *K. rhytiphora* and *K. peroni* are more closely related to one another than to *K. scalarina*. Intraspecific comparisons suggest that *K. peroni* from Oyster Harbour and Princess Royal Harbour are more genetically similar than those from Bruny Island, Tasmania reflecting their geographical proximity (Fig. 3). However, data from *K. scalarina* suggest greater affinities between geographically distant rather than close populations (Fig. 3). *Katelysia* from Augusta, which were described on conchological evidence as *K. scalarina polita* by Nielsen (1963), have banding patterns (Fig. 2 & 3) more closely resembling those of *K. scalarina* than either *K. rhytiphora* or *K. peroni*.

2) Anatomy

No gross anatomical differences were obvious on dissection of the three *Katelysia* species. However, microscopic examination revealed a more complex appearance of the mantle margin in *K. scalarina* than in the other species. This is clearly seen in SEM preparations of the mantle margin of the three species (Fig. 4). In all three species the middle mantle fold terminates posteriorly in a protrusion near the siphons. Protrusion development is least in *K. peroni* which has irregular marginal processes (Fig. 4a) and greatest in *K. scalarina* which has regular tentacular marginal processes 3-400μm long (Fig. 4c). In *K. rhytiphora* the protrusion is somewhat intermediate between these conditions in having short (2-300μm) regular marginal processes (Fig. 4b). The ventral part of the middle mantle fold has no major processes in either *K. peroni* or *K. rhytiphora* (Fig. 4d, e) but in *K. scalarina* the processes seen on the posterior mantle protrusion extend a short way anteriorly along the inner mantle fold, becoming more irregular and smaller as they do (Fig. 4e). Anteriorly, close to the anterior adductor muscle all three species bear processes on the middle mantle fold and these show species differences similar to those on the posterior part, being best developed in *K. scalarina* and least devleoped in *K. peroni*.

3) Seasonal Population and Reproductive Changes

Size frequency distributions were based on variable and sometimes very small samples and must be interpreted with caution. Largest samples throughout were for *K. scalarina* from Princess Royal Harbour and for several months from November 1978 to June 1979 this species showed bimodal samples indicative of two size (and presumably age) classes (Fig. 5). The growth of these size classes is indicated by lateral shift of the model peaks which appear to have merged by July 1979. In August 1979 the start of a new recruitment phase is suggested by the presence of a small peak representing animals $>$ 1 cm long. The sample for September 1978 is considered inadequate because sampling did not involve sieving and so would have tended to miss small animals. Monthly sample sizes for *K. rhytiphora* from Princess Royal Harbour were generally small but the major peak throughout the study period represented animals between 3 and 4.5 cm shell length and no major influx of small animals was recorded. Although sampling was not started until February 1979 the situation in Oyster Harbour appeared almost to be the reverse with *K. scalarina* showing unimodal samples throughout. In *K. rhytiphora*, however, an influx of small individuals in March and April 1979 which possibly resulted from the spawning before October 1978 resulted in bimodal samples during the latter half of the study period.

Monthly gonad indices (Fig. 6) suggest differences between species and localities. The Princess Royal Harbour populations of *K. scalarina* showed a clear spawning period between April and June 1979 and, although not so marked, there was some evidence of spawning during the period in the Oyster Harbour population of this species (Fig. 6). Gonad indices for *K. rhytiphora* from Oyster Harbour pointed to a major spawning before October 1978. In Princess Royal Harbour gonad indices for *K. rhytiphora* were increasing between September 1978 and January 1979 which also suggests previous spawning. The irregular samples of *K. peroni* taken during the study period do not offer an adequate data base for any firm conclusions about periods of spawning in this species. However, gonad indices for *K. peroni* were declining between September and January in Princess Royal Harbour and between January and July in Oyster Harbour.

4) Distribution

The considerable overlap in vertical distribution of the three species of *Katelysia* is clearly illustrated in Fig. 7. *K. scalarina* extends slightly higher up the shore than the other species which appear to occupy similar vertical ranges (Fig. 7). Differences in zone position between the two sites may have arisen from topographical differences as *Katelysia* was found exposed more frequently in Oyster Harbour than in Princess Royal Harbour. *Katelysia* densities in the zones of maximal species overlap ranged from about 100 to 500 m^{-2}. Relative proportions of the three species (Fig. 8) of *Katelysia* indicate that *K. scalarina* is the most abundant species in Princess Royal Harbour while *K. rhytiphora* tends to be more common in Oyster Harbour. Small numbers of *K. peroni* occur sporadically in both harbours.

DISCUSSION

The application of electrophoretic techniques to bivalves has, in the majority of recent studies, been aimed at elucidating intraspecific protein polymorphisms (Murdoch, Ferguson & Seed, 1975; Levinton & Koehn, 1976; Ahmed, Skibinski & Beardmore, 1977; Morgan, Block, Ulanowicz & Buys, 1978; Beaumont, Day & Gage, 1980; Beaumont, 1982). In a few cases, however, electrophoresis has been used to separate closely related bivalve species and to investigate their degree of overlap (Pesch, 1974; Brock 1978; Skibinski & Beardmore, 1979; Hornbach, McLeod, Guttman & Seilkop, 1980; Gosling & Wilkins, 1981). Davis (1983) ranks the relative value of taxonomic data sets for North America unioids as follows; allozyme data $>$ comparative anatomy $>$ conchology. Although comparisons based on total protein pattern are not as useful as those based on locus-by-locus analyses (Ferguson, 1980) they do offer additional, possibly more objective, information to conchology and comparative anatomy for assesing taxonomic relationships. General protein patterns of *Katelysia* samples from a variety of localities lend support to the view that the three described species are distinct and valid. Despite its distinct shell form the sub-species *polita* described by Nielsen (1963) can be confirmed as *K. scalarina* but no comment on its degree of separation or whether it merits sub-specific status may be made without more detailed study.

Differences in shell morphology between the three species *K. scalarina, K. rhytiphora* and *K. peroni* are described by Cotton (1961). Where whole animals are difficult to separate on shell characteristics alone they may be distinguished by differences recorded above in the middle mantle fold. The middle fold of the mantle edge in bivalves is largely receptive in function (Yonge, 1957) and it may be assumed that tentacle development reflects the degree of marginal sensory development. Ansell (1981) has reported differences in tentacle development on the middle mantle fold between two species of *Donax* from South Africa but offered no possible reasons for these differences.

Since fertilization in bivalves is predominantly by gamete broadcast, reproductive isolation in closely allied sympatric species is frequently maintained by seasonal differences in their reproductive cycles. This has been well demonstrated by Seed (1971) for populations of *M. edulis* and *Mytilus galloprovincialis* Lamarck from south western England. Although they overlap, the autumn/winter spawning period of *K. scalarina* and the winter/spring spawning period of *K. rhytiphora* seem sufficiently different to minimize the possiblity of hybridization. No great reliance can be placed on the proposed spring or late summer spawning periods of *K. peroni* as they are based on very small samples. However, the available data point to a spawning period distinct from those of the other two species. By contrast Nielsen (1963) found that in Mornington, Victoria the major spawning periods for *K. scalarina* and *K. rhytiphora* were September-October and September-November (spring) respectively with *K. rhytiphora* showing a second large spawning in March. Despite this large overlap in the spawning periods, laboratory attempts to hybridize the two species were unsuccessful so that there are probably physiological barriers which prevent thier interbreeding (Nielsen, 1963). Taken together with available population data the spawning patterns suggest that in Princes Royal Harbour recruitment levels for *K. rhytiphora* are low while those for *K. scalarina* are relatively high whereas in Oyster Harbour the situation is reversed. These observations partly explain why *K. rhytiphora* is more common in Oyster Harbour. Population size frequency data presented by Coleman (1982) for *K. rhytiphora* in Western Port, Victoria point to low level recruitment, mainly between December and March. This is after the major spawning period proposed by Nielsen (1963) for Mornington, Victoria. In Oyster Harbour *K. rhytiphora* spat appear in March and April byssally attached to the adults. Recruitment in *K. peroni* is probably low in both harbours. as evidenced by its uncommonness and the absence of small individuals in samples of this species.

Distributional information given by Nielsen (1963) and supported by personal observations indicate that although all three species occur, at varying relative densities, in suitable habitats along almost the entire southern coast of Australia, *K. rhytiphora* and *K. peroni* reach their western limits in Princess Royal Harbour. Further westwards the populations of *K. scalarina* are exclusively of the shell form described by Nielsen (1963) as *K. scalarina polita.*

The three species of *Katelysia* seem to have very similar habitat requirements viz. shallow, sheltered soft bottoms. Such situations are common in numerous embayments along the southern coast of Australia and typically harbour populations of *Katelysia* species. One feature of these embayments is that they may, periodically, be cut off from the open sea as a result of the formation of sand bars by accumulated sediments at their openings (Hodgkin, pers. comm.). Under such circumstances a combination of the founder effect and changing environmental conditions could lead to fairly rapid genetic change. The majority of the resultant populations would not survive if the sand bars remained closed and genetic adaption could not keep pace with the ensuing environmental changes. However, if contact with the main *Katelysia* populations were restored (by opening of the sand bars) these trends would be reversed but with the possibility of effecting gene pool changes. A high level of intraspecific variation is indicated by electrophoresis (pers. obs.). Thus the genus *Katelysia* in southern Australia is comprised of opportunist (r-selection type) species ideally suited to exploit the variable environmental conditions in the region. Its success is reflected both in that it is often the major or only colonist of coastal embayments and in maintaining this dominant role where diverse communties become established. The present prelimary work demonstrates the need for a more detailed study of the genus *Katelysia* in Australia to clarify the problem outlined above. Such a study would, of necessity, be long term (say 5 years) in order to establish precise population and reproductive cycles and should ideally include physiological tolerance studies. In this context Oyster Harbour and Princess Royal Harbour provide the ideal localities as they contain breeding populations of the three known species at the distributional limits of two of them.

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Table 1. Coefficients of similarity (S_m) between samples of *Katelysia* species from different localities in southern Australia. Data shown are maximum values obtained from several tests using isolectric focussing on PAGs and staining for general proteins.

Species		*K. scalarina*				*K. rhytiphora*			*K. peroni*		
Species	Source	Tas.	O.H.	P.R.H.	Aug.	Tas.	O.H.	P.R.H.	Tas.	O.H.	P.R.H.
K. scalarina	Tas.	0.75	0.571	0.643	0.471	—	—	—	—	—	—
	O.H.		0.636	0.539	0.677	—	0.455	—	—	0.231	
	P.R.H.			0.632	0.529	—	—	0.375	—	—	0.389
	Aug.				0.667						
K. rhytiphora	Tas.					N.V.	—	—	—	—	—
	O.H.						0.714	0.476	—	0.385	—
	P.R.H.							0.563	—	—	0.524
K. peroni	Tas.								N.V.	0.556	0.5
	O.H.									0.385	0.667
	P.R.H.										0.412

Key: Tas. — Great Bay, Bruny Island, Tasmania; O.H. — Oyster Harbour, W.A.; P.R.H. — Princess Royal Harbour, W.A.; Aug. Augusta, W.A; N.V. — no value.

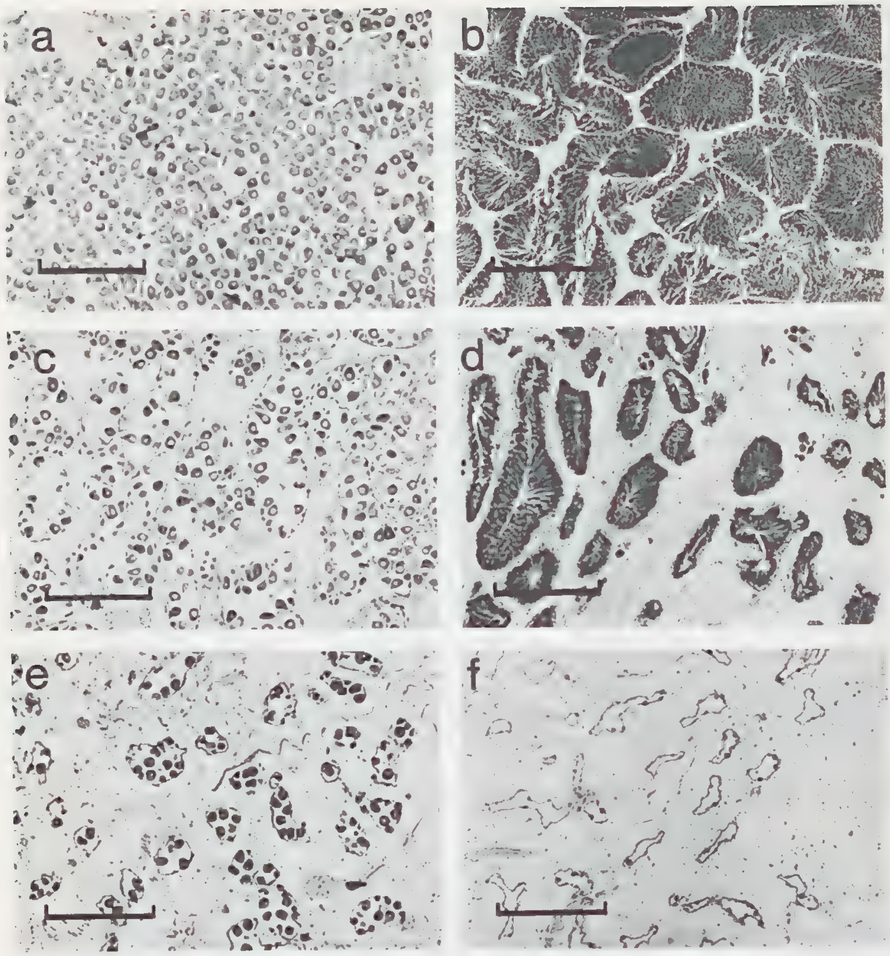

Fig. 1 Photomicrographs of sections of *K. rhytiphora* gonads stained with haematoxylin and eosin and showing some of the arbitrary numerical values assigned to various stages. No distinction was made between developing and regressing gonads. (a) Fully ripe female (stage 4). (b) Fully ripe male (stage 4). (c) Half spawned female (stage 3). (d) Three quarters spawned male (stage 2). (e) Female gonad nearing the end of spawning (stage 1). (f) Completely spent gonad of uncertain sex (stage 0). Scale = 500 µm.

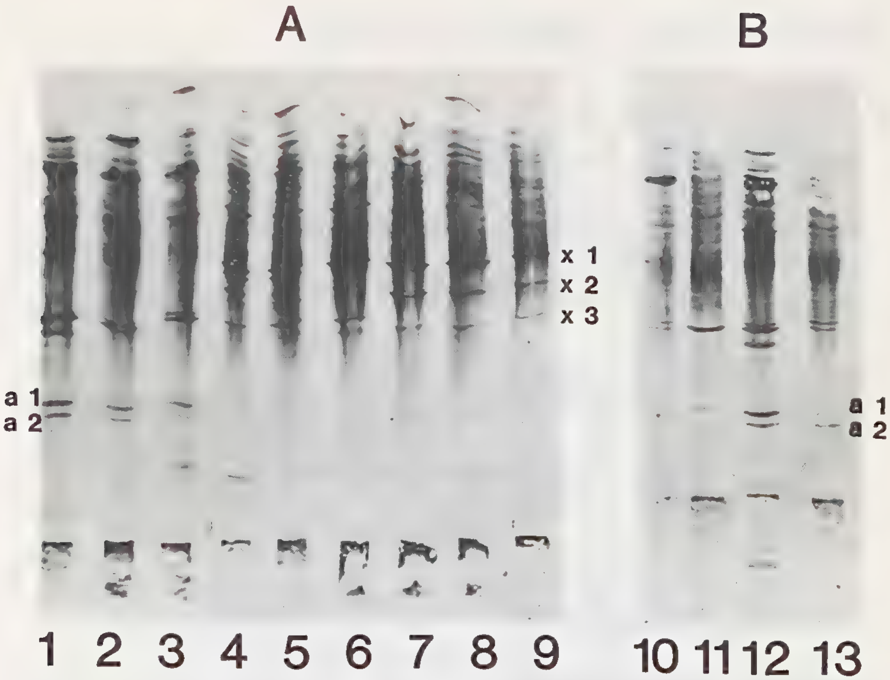

Fig. 2 General protein patterns of whole extracts of *Katelysia* species from southern Australia as separated by isoelectric focussing on a pH gradient 3.5-9.5 (highest pH at top of photograph). A) Sympatric samples from Oyster Harbour of *K. scalarina* 1,2,3, *K. rhytiphora* 4,5,6 and *K. peroni* 7,8,9. B) Allopatiric samples of *K. scalarina* from Princess Royal Harbour, Western Australia 10, Bruny Island, Tasmania 11, Oyster Harbour, Western Australia 12 and Augusta (= *K. scalarina polita* Nielsen, 1963), Western Australia 13. a_1, a_2, bands of common mobility in *K. scalarina*; x_1, x_2, x_3 bands of common mobility in *K. peroni*.

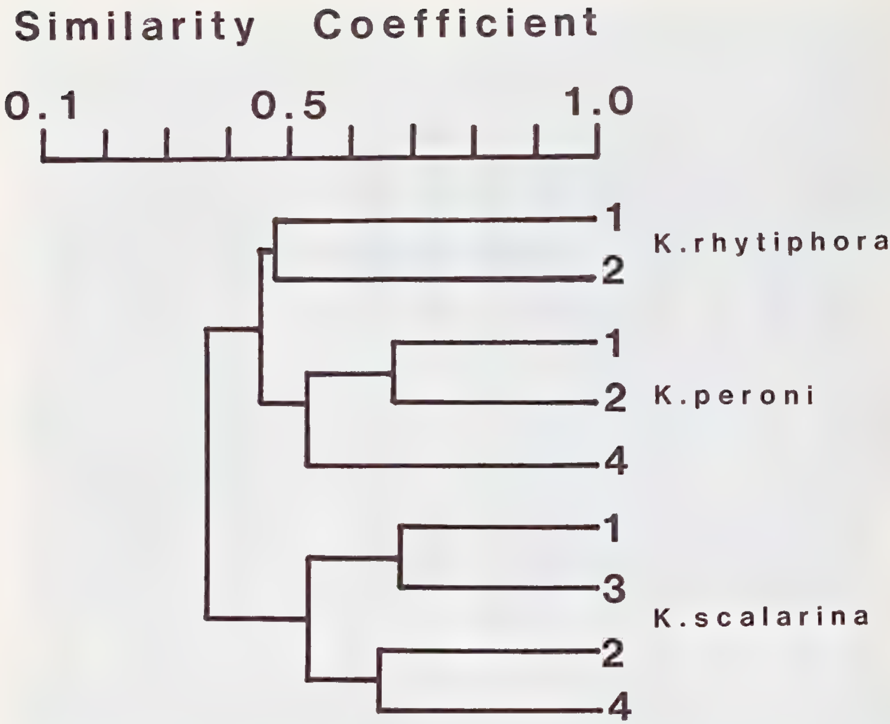

Fig. 3 Phenogram showing proposed relationships, based on general protein patterns, between species of *Katelysia* from Oyster Harbour (1), Princess Royal Harbour (2), Augusta (3), Western Australia and Bruny Island, Tasmania (4). The dendrogram was constructed by unweighted pair group arithmetic average (UPGMA) cluster analysis.

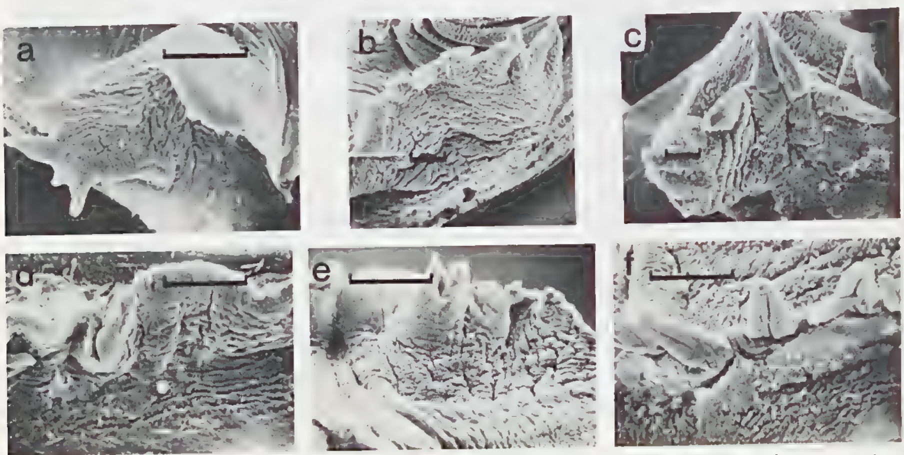

Fig. 4 S.E.M.s of the middle mantle folds of *Katelysia* species showing the posterior regions (*d, e, f*) and their protrusions (*a, b, c*) in *K. peroni* (*a, d*) *K. rhytiphora* (*b, e*) *K. scalarina* (*c, f*). Scale = 250 μm.

Fig. 5 Percentage size-frequency distributions of anterior-posterior shell lengths for *K. scalarina* ☐ and *K. rhytiphora* ■ from Princess Royal Harbour and Oyster Harbour, Western Australia, September 1978-August 1979. n.s., no sample. Numbers in parentheses = sample size. Length scales in centimetres.

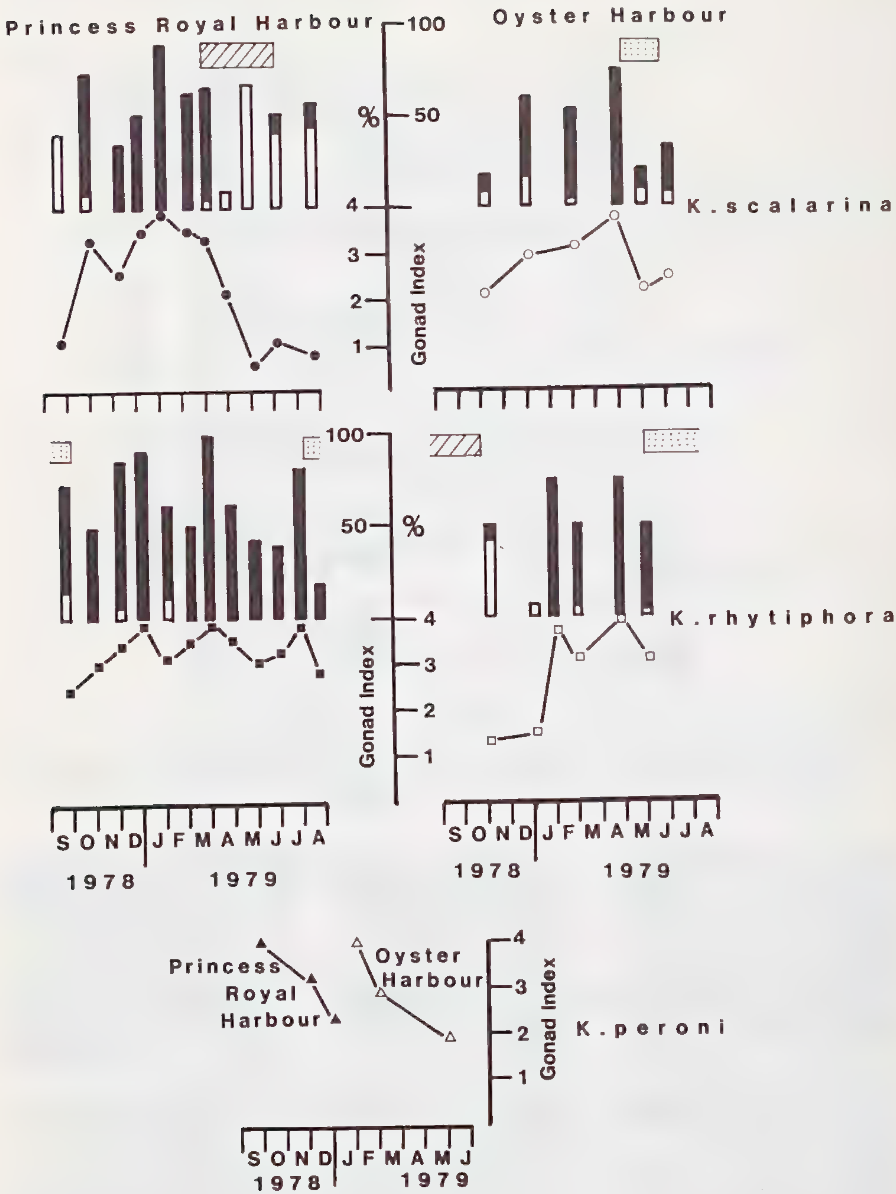

Fig. 6 Reproductive cycles and proposed spawning periods of *Katelysia* species from Princess Royal Harbour and Oyster Harbour, Western Australia 1978-79. The gonad index and the percentage of ripe and spent animals for each monthly sample are shown (☐ spent or stage 0, ■ ripe or stage 4, ▨ major spawning, ▦ minor spawning).

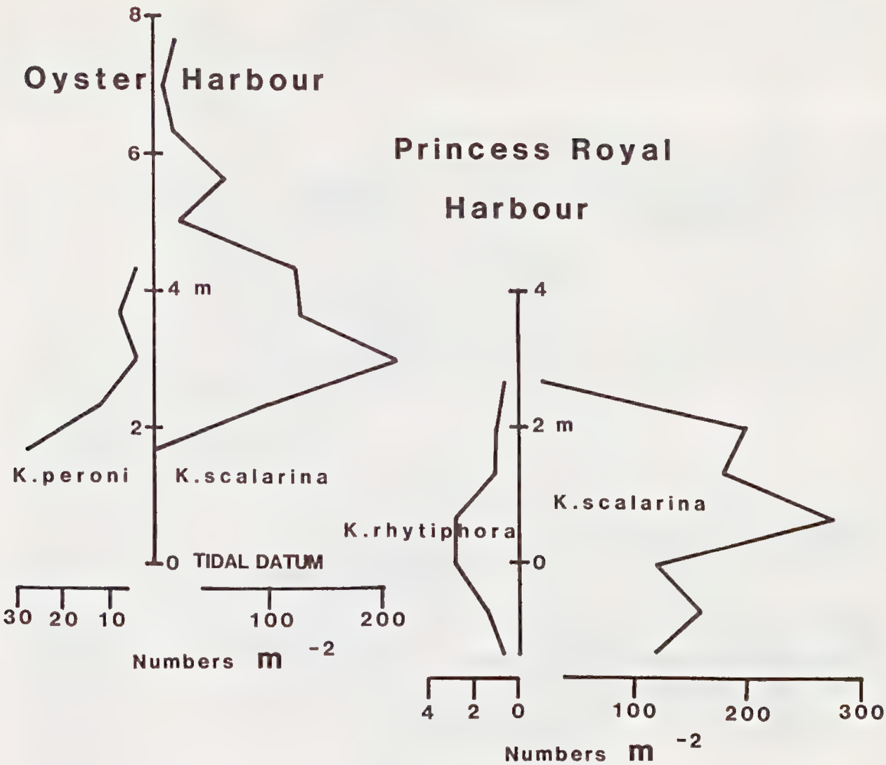

Fig. 7 Zonation patterns of *Katelysia* species in A) Oyster Harbour (site 7, Fig. 8) and B) Princess Royal Harbour (site 1, Fig 8) relative to tidal datum. (Date based on Wells & Roberts, 1980 and Wells & Threlfall, 1980.

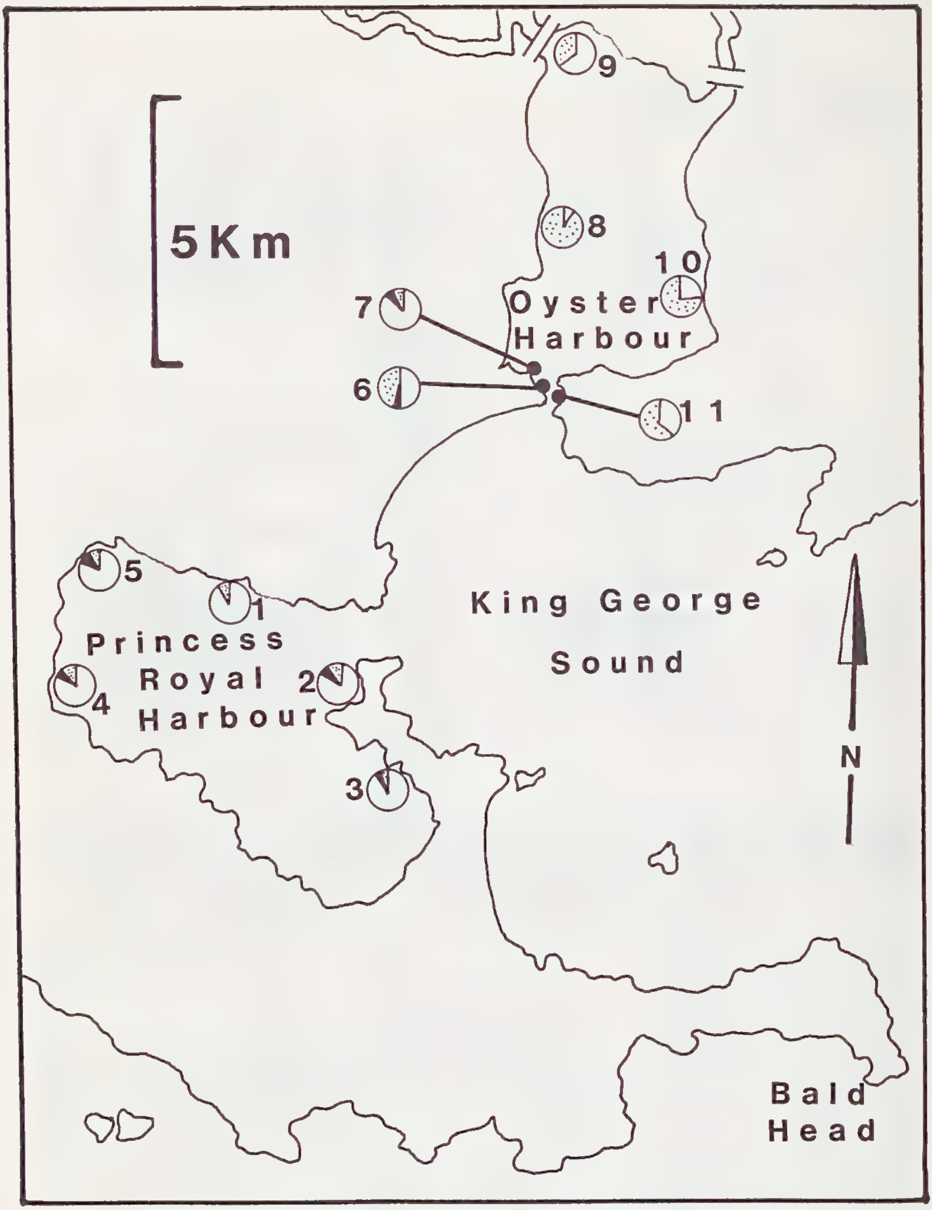

Fig. 8 Relative proportions of *K. scalarina* ○ , *K. rhytiphora* ◌ and *K. peroni* at selected sites in Oyster Harbour and Princess Royal Harbour, Western Australia.